Research paper

The Holocene
2016, Vol. 26(2) 302–313

DOI: 10.1177/0959683615608691
hol.sagepub.com
SAGE

Great Plains vegetation dynamics in response to fire and climatic fluctuations during the Holocene at Fox Lake, Minnesota (USA)

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Abstract

Vegetation composition and fire frequency are tightly linked in North American grasslands and have varied considerably throughout the Holocene in response to different drivers. Yet, detailed records of both long-term changes in grassland vegetation composition and diversity, coupled with fire history, are still relatively sparse. In this study, we examine a sediment core from Fox Lake, Minnesota, using pollen, charcoal, magnetic susceptibility, organic carbon (%C), and silica (%Si) records with the aim of understanding grassland structure and function during the Holocene, particularly in the context of vegetation composition and diversity, erosion, and fire activity. Nonarboreal pollen comprises between 37% and 86% of the assemblage throughout the record with the largest percentages occurring during the mid-Holocene (~8000–4000 yr BP). The pollen record also suggests that at 8200 yr BP, there was an abrupt shift from oak-elm woodland to a more open landscape of grassland or savanna, which remained throughout the mid-Holocene. Additionally, the pollen data suggest that vegetation composition exhibited little change in diversity through time despite recurring fire. Charcoal concentrations varied from 30 to nearly 1200 particles cm^{-3}, indicating changes in relative amount of biomass burned, but the morphotypes of charcoal pieces indicate that woody fuels persisted during the mid-Holocene despite the apparent grassland-dominated landscape. Magnetic susceptibility in the sediment ranges from −0.9 to 22.4 ($\times 10^{-5}$ SI) throughout the record, with the biggest increase occurring as the vegetation shifted from woodland to grassland entering the mid-Holocene. Organic carbon ranges from 4.6% to 20.0% and exhibits a slow but steady increase after the 8200 yr BP event. Silica decreases slightly but remains generally high between 20.4% and 22.5%.

Keywords

charcoal morphotypes, climate change, grassland biodiversity, Great Plains, magnetic susceptibility, pollen

Received 11 April 2015; revised manuscript accepted 10 August 2015

Introduction

North American grasslands have experienced extreme climate variability with respect to temperature and moisture throughout the Holocene: multi-decadal megadroughts (Booth et al., 2005; Cook et al., 2010; Laird et al., 1996a) as well as shorter duration droughts (Borchert, 1950). In the Great Plains region of the United States, the mid-Holocene (approximately 8000–4000 yr BP) was generally characterized by warmer temperatures, less moisture, and extreme fluctuations between moist and arid phases (Grimm et al., 2011; Schmieder et al., 2013) compared with the early or late-Holocene. Current projections of climate change indicate that extreme phases like these are expected to increase in frequency and intensity in the future (IPCC, 2014). However, prediction of possible responses of grassland vegetation and fire to future climate change scenarios requires an understanding of responses of vegetation and fire to climate changes throughout the past. While climate is a regional driver of vegetation and fire, local differences exist in how vegetation and fire respond (Camill and Clark, 2000; Power et al., 2008). Additionally, previous work suggests that climate may affect fire regimes indirectly through vegetation composition and productivity, rather than through a direct link (Camill et al., 2003; Clark et al., 2001), making it critical to understand these systems in the context of each other.

In the northern Great Plains, substantial climatic and vegetation changes occurred during the Holocene and have been noted in many records across the region, including the vegetation shift from deciduous woodland to grassland entering the mid-Holocene due to an increase in regional aridity (Baker et al., 1992, 2002; Grimm et al., 2011; Laird et al., 1996b; Van Zant, 1979). However, vegetation changes throughout the Holocene have often been asymmetrical with climate change through time. For example, the shift from woodland to grassland at the onset of the mid-Holocene was quite abrupt in most records, while the increased presence of woody species during the late-Holocene was relatively gradual (Umbanhowar et al., 2006). It is well established that grassland ecosystems dominated much of the Northern Great Plains throughout the mid-Holocene and into the late-Holocene

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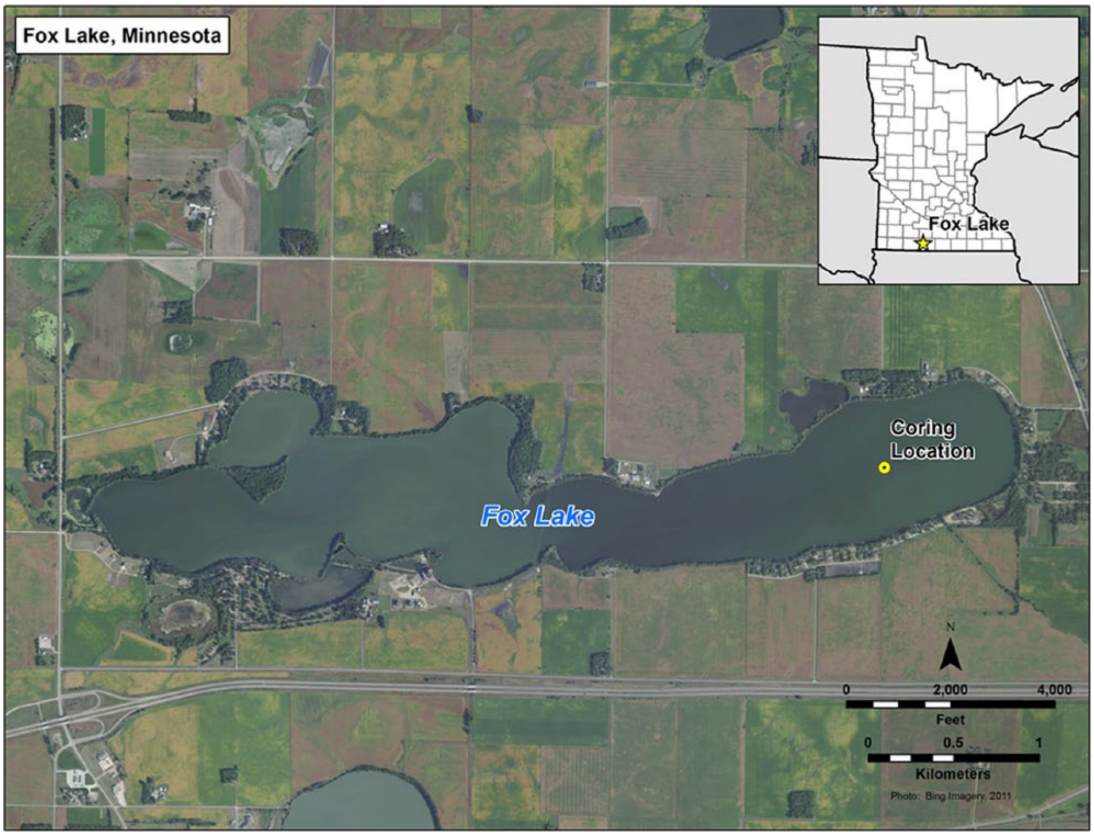

Figure 1. Fox Lake, Minnesota. Coring location is shown by the dot on the main figure. Inset figure shows the location of Fox Lake within Minnesota.

(Baker et al., 2002; Camill et al., 2003; Van Zant, 1979; Watts and Bright, 1968); however, their composition and floristic diversity relative to forested times has not been investigated. Furthermore, examination of grassland composition and diversity in the context of the rapid climate fluctuations of the Holocene can provide insight into the functions and processes involved in grassland ecosystems on a broad temporal scale.

Grassland fire regimes have generally been interpreted to consist of high-frequency, low-intensity events and seem to produce high charcoal concentrations in lake sediments (Grimm et al., 2011; Umbanhowar et al., 2009). However, the fuel sources for grassland fires as interpreted through charcoal morphology (Jensen et al., 2007; Lynch et al., 2006) are likely mixtures of arboreal and nonarboreal sources. Fire has been a major component of grassland ecosystems of North America, and regular fire activity has been shown to be crucial in maintaining grasslands by inhibiting the invasion of woody plants, such as *Quercus* sp. (Briggs et al., 2005; Danner and Knapp, 2001). Nevertheless, understanding the relationship between fire and vegetation in grasslands, particularly during the Holocene, is complex. Fire frequency can increase during arid times if fuel condition is ideal or decrease during arid times if fuel quantity is limited (Nelson et al., 2012). At Kettle Lake, North Dakota, fire activity increased during the intermittent humid phases of mid-Holocene due to higher fuel loads and decreased during the predominant arid phases as a result of discontinuous and decreased vegetation cover (Grimm et al., 2011), suggesting that fuel quantity was the limiting factor rather than fuel quality.

Additionally, extremely arid phases with discontinuous vegetation and bare ground have been found to prompt soil mobilization at some locations across the Great Plains (Miao et al., 2007; Schmieder et al., 2013) which could have destabilized the landscape and further complicated the relationships between grassland vegetation and fire. In lacustrine sediments, magnetic susceptibility has become an increasingly utilized proxy for interpreting erosion activity during different phases of wet and dry conditions, although interpretation is not always straightforward (Geiss et al., 2003, 2004; Lascu et al., 2012; Schwalb et al., 2010). Magnetic susceptibility values can vary greatly depending on the severity of drought, from high levels during severe droughts to low levels in moderate droughts (Lascu et al., 2012). Geiss et al. (2003) found high magnetic susceptibility levels in sediment at lakes near the prairie-forest ecotone in Minnesota resulting from increased clastic deposition during mid-Holocene droughts. Given the long-standing history of droughts in the region (Booth et al., 2005; Cook et al., 2010; Laird et al., 1996a), a holistic understanding of these processes achieved through a multi-proxy study using both magnetic and nonmagnetic proxies is needed.

In this study, we present a high-resolution multi-proxy reconstruction of the paleoecological history at Fox Lake, Minnesota, with the aim of understanding grassland structure and function during the Holocene, particularly in the context of vegetation composition and diversity, erosion, and fire activity. We use pollen, charcoal, magnetic susceptibility, organic carbon, and silica proxies from lake sediment to achieve four main objectives: (1) identify the major transitions in vegetation cover, fire, and erosion at Fox Lake throughout the Holocene during periods of rapid climate change; (2) understand grassland composition and diversity at this site; (3) assess changes in fire activity and fuel sources for those fires; and (4) examine the variation in erosion from the landscape as a function of vegetation cover. By doing so, we provide greater insight into the interactions between grassland vegetation and some of their characterizing factors that function on broad temporal scales, such as recurring drought and fire.

Study area

Fox Lake (43°40′35″N, 94°41′14″W) is located in southern Minnesota (Figure 1) and formed during the retreat of the Des Moines Lobe at the end of the Wisconsin glaciation about 12,000 years ago. The surface area of the lake is approximately

Table 1. Radiocarbon ages and calibrated age equivalents used in determining the age model for Fox Lake. Calibration was conducted using IntCal13 (Reimer et al., 2013) in CLAM 2.2 (Blaauw, 2010).

CAMS #	Depth (cm)	Material dated	Uncalibrated ^{14}C yr BP ± 1σ	Calibrated range (yr BP)
160884	85	Stem macrofossil	345 ± 30	370–471
160883	265	Stem macrofossil	1775 ± 30	1629–1788
160882	633	Charcoal particles	4770 ± 40	5400–4480
160881	726	Charcoal particles	5860 ± 40	6600–6738
160880	916	Charcoal particles	8220 ± 130	8880–9378

385 ha and has approximate dimensions of 5.5 km from west to east and 0.75 km north to south. At its deepest, Fox Lake has a water depth of 6 m (Minnesota Department of Natural Resources, 2014). The catchment of the lake is fairly flat with little topographic relief aside from a few small wetlands and kettle lakes to the north. Current land use near the lake primarily consists of not only row crop agriculture but also some mixed deciduous trees (*Quercus macrocarpa, Salix nigra*, and *Fraxinus pennsylvanica*), grasses, and forbs at the lake edges. The modern climate at Fox Lake is humid continental (Dfa), with hot summers, great seasonal temperature differences, and year-round precipitation (Köppen and Geiger, 1930). July and January mean monthly temperatures average 22°C and −9°C, respectively (PRISM Climate Group, Oregon State University, 2015). Average total annual precipitation is around 800 mm (PRISM Climate Group, Oregon State University, 2015). The lake was chosen for this study because (1) its location in the prairie biome of the northern Great Plains makes it an ideal place to study changes in grassland vegetation composition throughout the Holocene; (2) it is sufficiently deep to have contained water throughout the duration of the Holocene, thereby providing a good depositional and preservational environment for our target proxies; and (3) it is a grassland lake in the wettest current climate conditions for this biome; thus, its climate history is linked with well-documented changes in the position of the prairie-forest border during the mid-Holocene (Williams et al., 2010).

Methods

Field and chronology

In January 2012, 9.3 m of sediment taken in nine overlapping drives were extracted from the near-deepest part of the lake (Figure 1) using a combination of piston corers including a modified Livingstone corer (Wright, 1967). The core was transported to the National Lacustrine Core Facility (LacCore) at the University of Minnesota, where it was split into archive and working halves. Subsamples of sediment spaced throughout the entire core at measured depths were extracted for pollen and charcoal analysis. A total of 96 1-cm^3 subsamples were taken every 10 cm or less (approximately every 50–120 cal. yr) for pollen analysis and 233 1-cm^3 subsamples were taken every 4 cm (approximately every 15–40 cal. yr) for charcoal analysis. Plant macrofossils and charcoal were taken from the core for AMS ^{14}C dating, and their position within the core was recorded (Table 1).

The five uncalibrated ^{14}C dates of the macrofossils and charcoal were calibrated to calendar years before present (hereafter yr BP, with present as AD 1950) using IntCal13 (Reimer et al., 2013) in CLAM 2.2 (Blaauw, 2010). Calibrated dates were plotted against depth to produce the age–depth model (Figure 2) using a smoothed spline at a smoothing level of 0.3 as the interpolation method. A bootstrap method of 1000 iterations was performed to assess a 95% confidence interval around the curve.

Magnetic susceptibility

Volume-normalized magnetic susceptibility was measured at LacCore on the archive half of the core at 0.5-cm resolution using

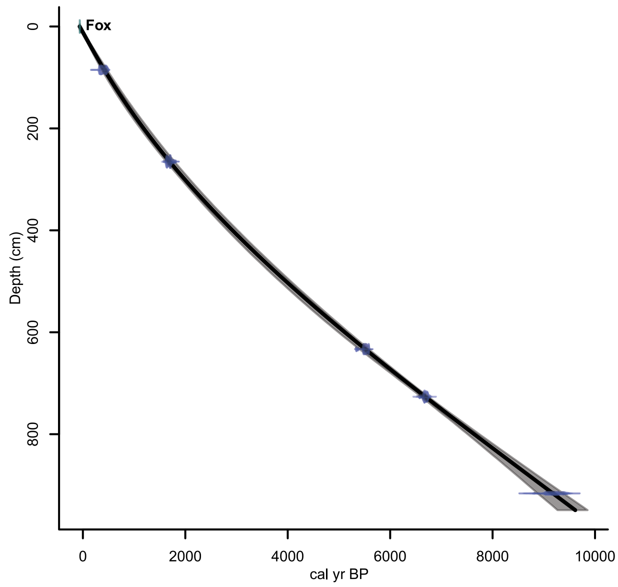

Figure 2. Age–depth model for Fox Lake, generated in CLAM (Blaauw, 2010).

a point sensor attached to a multi-section standard Geotek multi-sensor core logger. Magnetic susceptibility measures the abundance of ferromagnetic minerals, such as (titano)magnetite or maghemite, and has been interpreted as a proxy for clastic content within the sediment, delivered through erosion (Geiss et al., 2003). High values tend to indicate more magnetic minerals in the sediment and less organic material, as described by Lascu et al. (2010).

Magnetic susceptibility was chosen as the basis for zone delineation in this study because it provides unified information about multiple aspects of the ecosystem and integrates both the catchment and the lake. To delineate zones within the magnetic susceptibility data, a broken stick model was created and a constrained hierarchical cluster analysis was conducted in R statistical software (R Core Team, 2013) using the rioja package (Juggins, 2014) with Euclidean distance and constrained cluster analysis by the incremental sum of squares (CONISS) as the clustering method. The broken stick model was created through a segmented univariate regression on the magnetic susceptibility data, which separates the data into intervals and fits a separate line segment to each interval. The best number of cluster groups is the point at which the sum of squares approaches 0. Six initial cluster groups were identified as the best fit. Next, the constrained hierarchical cluster analysis defined the cluster boundaries based on the number of groups entered (six, in this case) and by minimizing the sum of variances within the data. A Kruskal–Wallis ANOVA test was conducted on the six cluster groups at the 0.01 significance level to determine whether the means of the groups were statistically different overall. A Kruskal–Wallis post-hoc pairwise comparison tested for significant differences between the mean of each cluster group and the other groups. Because the pairwise comparison identified cluster group 2 and cluster group 3 as being not statistically different at $p = 0.01$, we combined those two groups to arrive at a total of five cluster groups or zones.

To determine whether any cross-relationships existed with other proxies, Pearson product–moment correlation coefficients of magnetic susceptibility with charcoal concentration, total pollen influx, arboreal pollen influx, nonarboreal pollen influx, and %C were calculated using VassarStats, and significance was assessed at $p = 0.05$ (Lowry, 2015).

Organic carbon and silica

Organic carbon and silica were used to understand the degree to which sediment deposition originated from organic sources. We measured carbon concentrations (%C), which are closely correlated with organic matter concentrations, on dried bulk sediment samples via combustion at the Kansas State University Stable Isotope Mass Spectrometry Laboratory (SIMSL) following established procedures with a Carlo Erba 1110 elemental analyzer with a Conflo II interface. Inorganic carbon concentrations were tested by application of HCl to dried sediments throughout the core and were negligible.

Silica (Si) was measured using a Cox Analytical Itrax x-ray Fluorescence core scanner at the Large Lakes Observatory at the University of Minnesota Duluth. The Si data were standardized in a three-step process that corrects for laboratory error (Si:MoCoh), for erosion (Si:Ti), and then transformed using NIST standards (to percent concentration). The transformed %Si values and %C values have been used as indicators of in-lake productivity.

Pollen analysis and data treatment

Pollen was isolated from each of the 1-cm^3 subsamples (96 total) using standard techniques (Faegri and Iversen, 1989), spiked with a known concentration of microspheres, and mounted in silicone oil. Each sample was examined under a light microscope and counted to a sum of at least 300 terrestrial grains. Each pollen grain was classified to the finest taxonomic resolution possible, generally following McAndrews et al. (1973). The raw counts were then converted to percentages using the sum of upland pollen types, and the results were graphed using Tilia (Grimm, 1993). In addition, pollen influx (grains $cm^{-2} yr^{-1}$) was calculated using the raw counts, microsphere totals, and sedimentation rates. Pollen diversity was estimated by two ways: first, by calculating the taxonomic richness of the pollen assemblages and, second, by inferring the compositional turnover of the pollen assemblages. Taxonomic richness was evaluated using the total number of pollen taxa present in each sample, plotted against age. This was conducted in R statistical software (R Core Team, 2013) using the vegan package and the decostand function (Oksanen et al., 2015). To infer the compositional turnover of the pollen assemblages based on the β-diversity (Hill and Gauch, 1980), an age-constrained detrended canonical correspondence analysis (DCCA) was used (Ter Braak, 1986). This was conducted with square-root transformed pollen percentages, detrending by segments, and nonlinear rescaling, following Birks (2007). Downweighting and no downweighting of rare taxa options were both tried initially; downweighting has traditionally been used for pollen turnover analysis (see Birks, 2007); however, no downweighting was selected in this study because of the many rare pollen taxa present in our data, and results were fairly similar between the downweighting and no downweighting options. A value of $\geqslant 4$ standard deviation (SD) units would imply complete turnover – a given pollen assemblage shares no taxa with the previous assemblage (Hill and Gauch, 1980). All aspects of the DCCA were conducted in Canoco 5 (Ter Braak and Smilauer, 2012).

Charcoal analysis

Macroscopic charcoal analysis was conducted on the 1-cm^3 subsamples (233 total) following the methods of Long et al. (1998). All samples were soaked in a 10% H_2O_2 solution for 48–72 h before being passed through 125- and 250-μm sieves. The sieved charcoal pieces were then placed in gridded petri dishes and identified under a dissection microscope according to the following morphotypes: (1) cellular (thin, rectangular, porous, and visible cell wall separations); (2) fibrous (thin and clumped bundles of filamentous charcoal); (3) dark (geometric in shape, thick, opaque, and with straight edges); (4) latticed (cross-hatched and rectangular); and (5) branched (dendroidal with jutting arms), generally following Jensen et al. (2007) and Mueller et al. (2014). Cellular and fibrous morphotypes correspond to grass and shrub (nonarboreal) fuel sources, while dark, branched, porous, and spongy morphotypes correspond to woody (arboreal) fuel sources. The total charcoal concentration (particles cm^{-3}), the charcoal concentration for particles larger than 250 μm, the charcoal concentration for particles larger than 125 μm but smaller than 250 μm, and the nonarboreal:total ratio of all counted particles were each plotted against age to examine the fire history and fuel sources. Charcoal particles larger than 250 μm were used to interpret local fire activity, while charcoal particles larger than 125 μm but smaller than 250 μm were used to interpret regional fire activity, following the findings of Whitlock and Millspaugh (1996). Various ways of distinguishing regional versus local fire exist with charcoal, yet most generally depend on the size of the charcoal particles (Aleman et al., 2013; Duffin et al., 2008). Charcoal influx was calculated by multiplying the total charcoal concentration and the sedimentation rate.

Our charcoal sampling plan focused on examining one sample every 4 cm and was designed because grasslands are known for experiencing annual or near-annual fire activity. This approach is different from other approaches that aim to reconstruct specific fire events, primarily those designed for forested ecosystems, which, therefore, typically utilize a continuous sampling plan. Our aim was not to reconstruct specific fire events, but rather focus on trends in the amount biomass burned and the fuel sources of those fires. Each 1-cm^3 section of sediment contained between 5 and 13 calibrated years of deposition, with 15–40 calibrated years of sediment between samples, depending on the sedimentation rate at the given position within the core. Similar discontinuous sampling plans have been used with success in other grassland work in this region (Umbanhowar et al., 2006).

Results

Magnetic susceptibility

Five statistically derived zones were delineated based on the magnetic susceptibility data (Figure 3). The approximate dates of each zone are as follows: zone 1 from 9300 to 7500 yr BP, zone 2 from 7500 to 5500 yr BP, zone 3 from 5500 to 3850 yr BP, zone 4 from 3850 to 1400 yr BP, and zone 5 from 1400 yr BP to present. As a whole, magnetic susceptibility is moderately inversely correlated with %C, but exhibits no correlative relationship to pollen or charcoal (Table 2). The magnetic susceptibility values throughout the record range from −0.9 to 22.4 ($SI \times 10^{-5}$), indicating a large range in the levels of ferrimagnetic minerals in the sediment throughout the Holocene. The largest range of values for any zone is exhibited in zone 1, when values increase from −0.3 to 22.4 ($SI \times 10^{-5}$). The greatest amount of intersample variability is in zone 2, between 7500 and 5500 yr BP, when values vary repeatedly between 5.6 and 22.3 ($SI \times 10^{-5}$). Immediately following that period, from 5500 to 1400 yr BP, values remain steadily low between 0 and 2 ($SI \times 10^{-5}$), indicating very low levels of ferrimagnetic minerals in the sediment during this time.

Zone 1 is characterized by steadily increasing magnetic susceptibility values until approximately 8000 yr BP when the values drop to around 6 ($SI \times 10^{-5}$) and begin to rise at 7850 yr BP (Figure 3). Zone 2 exhibits the highest amount of repeated variability in

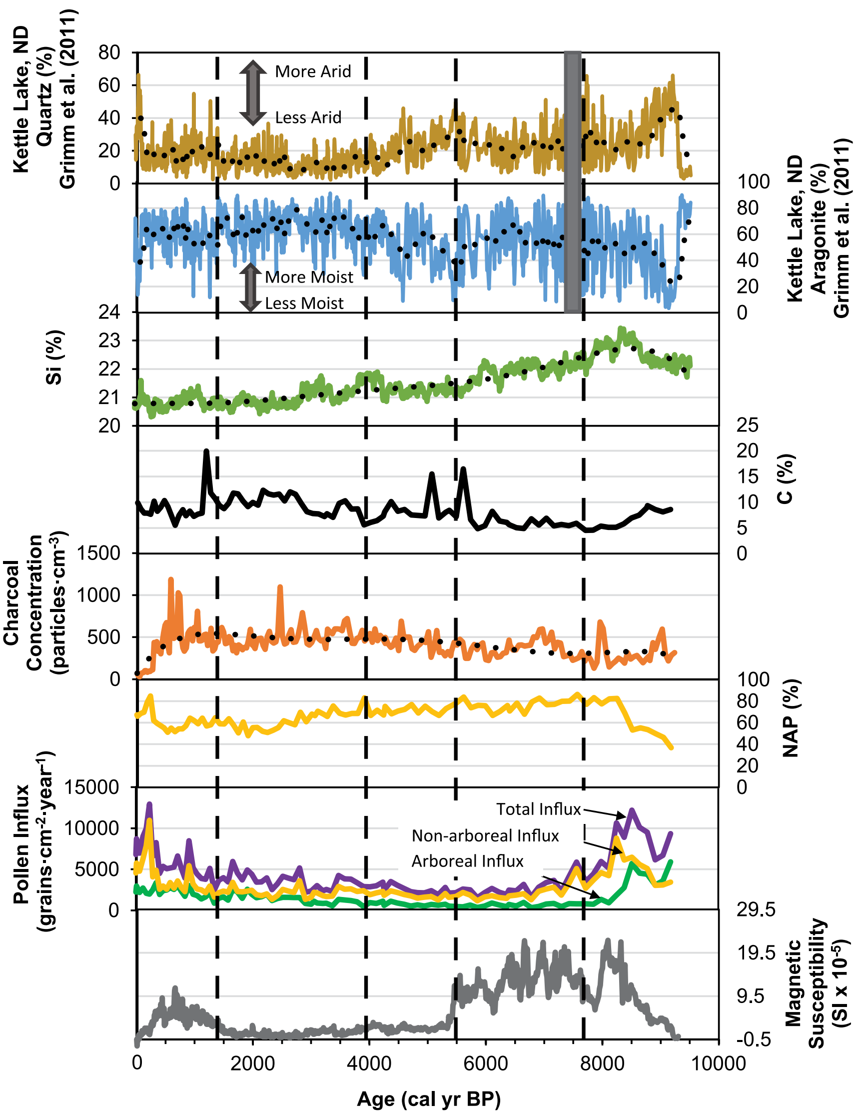

Figure 3. Summary of main proxies for Fox Lake, Minnesota (this article), in addition to quartz and aragonite from Kettle Lake, ND (Grimm et al., 2011), all plotted against age. From top to bottom: Kettle Lake %Quartz, Kettle Lake %Aragonite, Fox Lake %Si, Fox Lake %C, Fox Lake charcoal concentrations (particles cm^{-3}), Fox Lake %nonarboreal pollen, Fox Lake pollen influx (grains $cm^{-2}yr^{-1}$), Fox Lake magnetic susceptibility (SI × 10^{-5}). Dashed vertical lines indicate zones defined from constrained hierarchical cluster analysis on magnetic susceptibility data. Trendlines shown on Kettle Lake data (%quartz and %aragonite) were defined by a 25-period moving average fit. Trendlines shown on Fox Lake data (%Si and charcoal concentrations) were defined by sixth-order polynomial fit.

magnetic susceptibility values compared with the other zones, as the values increase and decrease many times (ranging between 5.6 and 22.3 (SI × 10^{-5})) throughout the zone. Zone 3 begins at 5500 yr BP and exhibits an initial decrease in values which stay relatively low (around 2.5 (SI × 10^{-5})) for the remainder of the zone with little variability. Zone 4 begins at 3850 yr BP, and magnetic susceptibility values remains consistently low (between 0 and 2.5 (SI × 10^{-5})) throughout the duration of the zone. Zone 5, the most recent zone, begins at 1400 yr BP with an increase in values that peak at 11 (SI × 10^{-5}) approximately 700 yr BP before steadily decreasing until the present. This zone displays a higher amount of temporal variability in magnetic susceptibility values than the previous two zones.

Organic carbon and silica

Carbon concentrations vary between 4.6% and 20.0% throughout the record (Figure 3). The lowest values occur at the end of zone 1 at approximately 8200 yr BP. Conversely, a generally increasing trend is exhibited after 8200 yr BP. As a whole, %C exhibits a moderate negative relationship with magnetic susceptibility (r=−0.53; Table 2) but relatively weak relationships with other proxies. %Si concentrations vary minimally (from 20% to 23.5%) throughout the record (Figure 3). The highest concentrations occur around 8300 yr BP and then steadily decrease throughout the duration of the record, although the lowest values are still relatively high at 20%.

Pollen

There is one major stratigraphic change (Figure 4), which encompasses a shift from dominant arboreal pollen to nonarboreal pollen at 8200 yr BP. After 8200 yr BP until present, when nonarboreal pollen dominated, arboreal pollen type generally consisted of less than 40% of the total pollen. The lowest values of arboreal pollen in the record were 14% at 7550 yr BP, and the highest values of arboreal pollen were 63% at 9160 yr BP. Overall, the most common pollen types in the record are *Ambrosia* sp., *Artemisia* sp., undifferentiated Asteraceae, Chenopodiaceae, Poaceae, *Pinus* sp., *Quercus sp.*, and *Ulmus* sp., comprising between 82% and 97% of the total assemblage. Total pollen influx is highest at the bottom (around 8500 yr BP) and the top (around 215 yr BP) of

Table 2. Pearson product–moment correlations of magnetic susceptibility, pollen, charcoal, and %C proxies.

	Magnetic susceptibility	Total pollen influx	Nonarboreal pollen influx	Arboreal pollen influx	Charcoal concentration	%C
Magnetic susceptibility	–	−0.02	0.07	−0.18	−0.19	**−0.53**
Charcoal concentration	−0.19	**−0.31**	**−0.41**	−0.06	–	0.20
%C	**−0.53**	0.01	−0.11	0.21	0.20	–

The values in boldface are significant at $p<0.05$. Degrees of freedom = 92 for all comparisons.

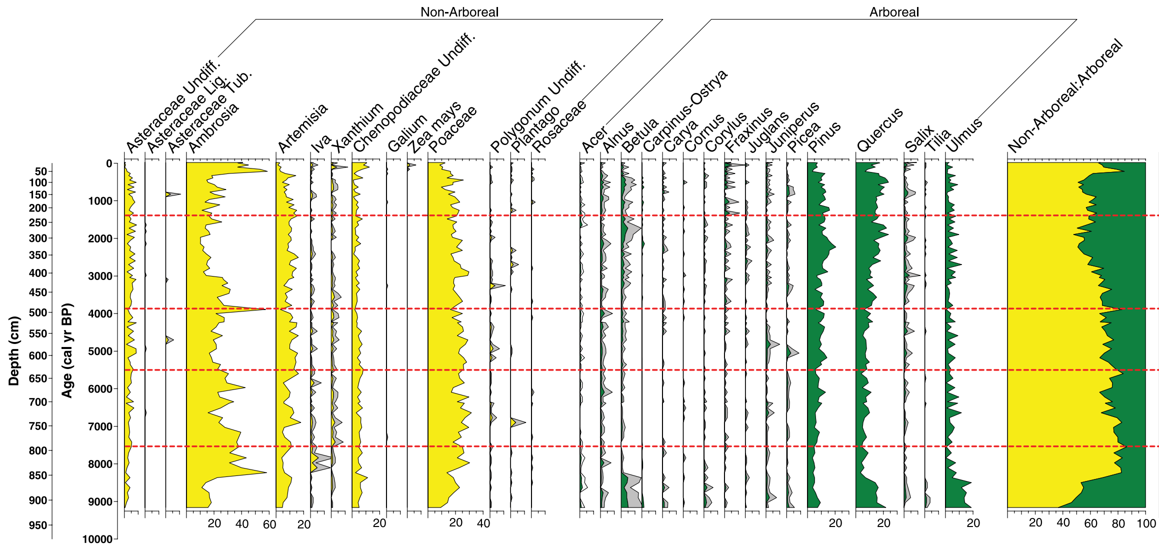

Figure 4. Pollen percentages of dominant terrestrial pollen taxa for Fox Lake, Minnesota, plotted against age and depth. Nonarboreal taxa are shown in yellow, and arboreal taxa are shown in green. Dashed lines indicate zones defined from constrained hierarchical cluster analysis on magnetic susceptibility data (see Figure 3).

the record, with the lowest values occurring toward the middle of the record from approximately 7000 to 5000 yr BP.

The compositional shift at 8200 yr BP is characterized by a sharp peak in *Ambrosia* pollen (from 10% to nearly 60%; Figure 4). The increase in *Ambrosia* is preceded by a more gradual increase in *Artemisia* (from 5% to 10%) and is shortly followed by an increase in *Iva* (from near 0% to 5%). Poaceae initially decreases at 8200 yr BP (from approximately 17% to 12%) and then increases to 30% and remains generally unchanged for much of the record. From 8200 to 5500 yr BP, Poaceae and *Ambrosia* are the most abundant taxa, with *Ambrosia* exhibiting more temporal variability and a greater range in relative abundance (between 15% and 45% of the total pollen sum) compared with Poaceae (between 15% and 30%; Figure 4).

From 5500 to 1400 yr BP, nonarboreal taxa continue to be the most abundant overall, generally comprising between 50% and 80% of the total pollen sum, but there is a gradual increase in arboreal taxa (Figure 4). The highest value of *Pinus* pollen abundance (20%) occurs around 2300 yr BP and is shortly followed by a peak in *Quercus* (25%) around 2000 yr BP. Another significant feature during this time is the sharp peak in *Ambrosia* (60%) at 3850 yr BP that decreases immediately thereafter.

At approximately 300 yr BP, several indicators of increasing disturbance on the landscape are recorded in the pollen assemblages. *Ambrosia* pollen increases dramatically to nearly 60% following an increase in *Artemisia* to 15%, similar to the event at 8200 yr BP (Figure 4). *Xanthium* and Chenopodiaceae pollen both increase at this time, to approximately 3% and 12%, respectively. In addition, *Zea mays* pollen appears for the first time in the record.

Neither pollen-type richness nor turnover changes when the pollen abundance shifts from predominantly arboreal to predominantly nonarboreal at 8200 yr BP (Figure 5a and b). Furthermore, neither richness nor turnover varies with age throughout the entire record. Richness (pollen taxa per sample) ranges between 13 and 30 throughout the record, with an average of 20 and SD of 3.6. However, the range of richness values is generally largest during the middle Holocene and beginning of the late-Holocene (zones 3 and 4), although in zone 4, this could be attributed to the greater number of samples in the zone because it covers the largest amount of time (3850–1400 yr BP) than any of the other zones. The range of taxonomic richness values for each zone is as follows: 17–26 taxa per sample in zone 1, 15–25 taxa in zone 2, 13–27 taxa in zone 3, 16–30 taxa in zone 4, and 16–28 taxa in zone 5. Throughout the record, the majority of samples have a turnover of less than 1 SD unit (4 SD units would be full turnover). This suggests that the pollen assemblage composition was not drastically changing throughout time, despite the changes in abundances of arboreal and nonarboreal taxa. Two samples have a turnover value higher than 2 SD units: 2.2 at 5845 yr BP and 2.4 at 50 yr BP, and seven samples have a turnover value higher than 1.5 SD units; however, turnover values repeatedly return to 1.0 or lower, suggesting that community composition stabilized after each of these instances.

Charcoal

The charcoal data are highly variable throughout the record with regard to both the amount and type of charcoal (Figure 6a–c). Total charcoal concentrations (Figure 6a) generally stay below 500 particles cm^{-3} from 9200 to 7500 yr BP, with the exception of one peak (600 particles cm^{-3}) at 9000 yr BP and another peak (about 700 particles cm^{-3}) at 7950 yr BP. Between 7500 and 5500 yr BP, there is a gradual increase from 250 to 600 particles cm^{-3} at 6900 yr BP and then a general decline to 250 particles cm^{-3} by 6000 yr BP. Total concentrations then begin to increase and continue to increase through the next zone (5500–3850 yr BP). As a whole, total charcoal concentration

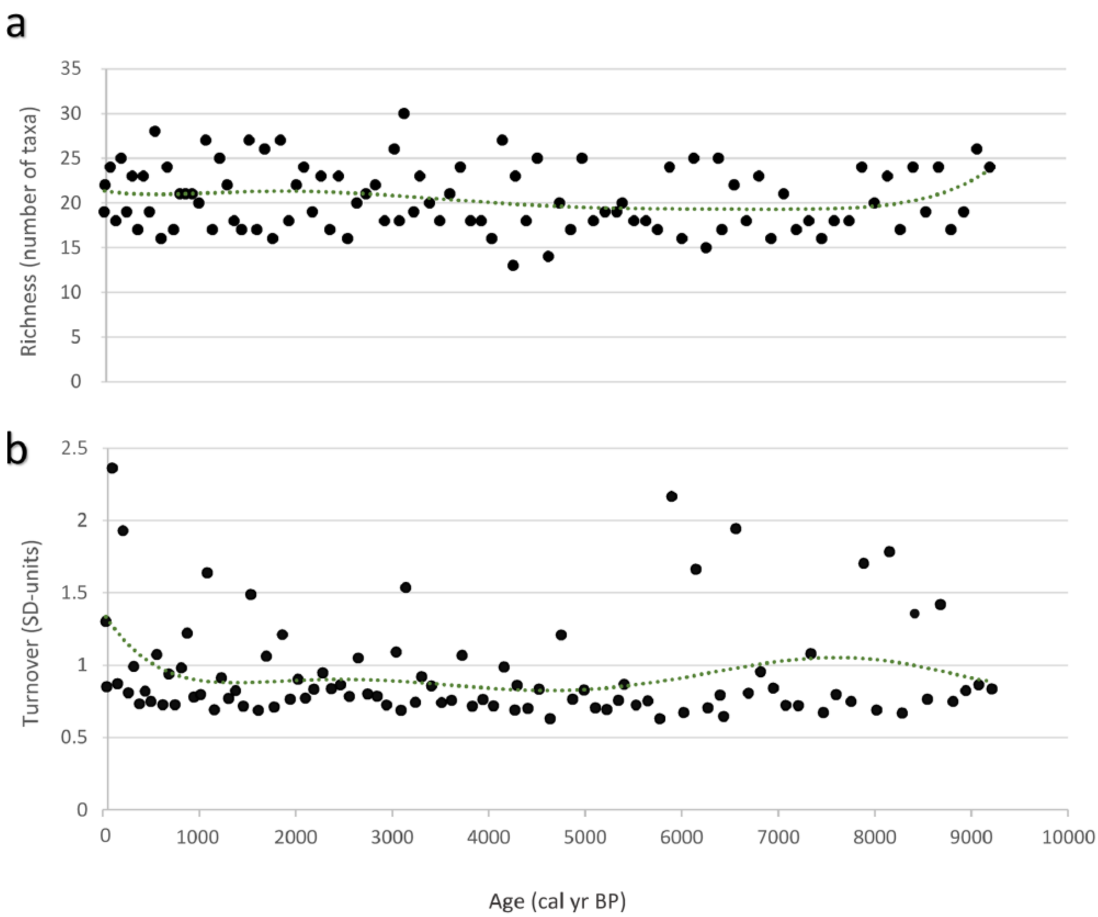

Figure 5. Pollen assemblage richness and turnover at Fox Lake, Minnesota. Trendlines were defined by a sixth-order polynomial fit. Panel (a) portrays taxonomic richness (number of taxa present in a sample) and panel (b) portrays turnover (SD units) with age. Higher SD values represent higher turnover of pollen taxa from one sample to the next sample in the chronology.

exhibits a moderate inverse correlation with total pollen influx and nonarboreal pollen influx but no relationship with arboreal pollen influx (Table 2).

From 3850 to 1400 yr BP, total charcoal concentrations fluctuate around 500 particles cm^{-3} but exhibit a larger amount of temporal variability (SD of 122.4 particles cm^{-3}) relative to the previous zone (SD of 96.8 particles cm^{-3}; Figure 6a). One sample in this zone at approximately 2200 yr BP has 1100 charcoal particles, the largest number of particles relative to any earlier time in the record. From 1400 yr BP to present, the charcoal data exhibit the greatest amount of temporal variability in the record (SD of 249.9 particles cm^{-3}). In addition, three samples have concentrations higher than 900 particles cm^{-3}: 1187 particles cm^{-3} at 560 yr BP, 1027 particles cm^{-3} at 690 yr BP, and 991 particles cm^{-3} at 710 yr BP.

Low concentrations of the local charcoal (larger than 250 µm in size; Figure 6a) are exhibited in the early part of the record from 9200 to 7500 yr BP. This signal is not distinguishable in the regional charcoal (larger than 125 µm but smaller than 250 µm in size; Figure 6a). From 7500 to 1400 yr BP, the local charcoal concentrations exhibit greater temporal variability (SD of 45.2 particles cm^{-3}) and are higher on average than the early part of the record (Figure 6a). From 1400 yr BP to present, they exhibit the highest temporal variability than during any other zone (SD of 76.8 particles cm^{-3}; Figure 6a). The highest (384 particles cm^{-3}) and lowest (2 particles cm^{-3}) concentrations of local charcoal particles throughout the entire record also occur between 1400 yr BP and the present.

Charcoal influx ranges between 5 and 190 particles $cm^{-2} yr^{-1}$ throughout the record (Figure 6b) and shows steadily increasing values from the early part of the record toward present, similar to the charcoal concentration data. The lowest temporal variability in charcoal influx occurs in zones 1 and 2 (SD of 9.8 and 9.1 particles $cm^{-2} yr^{-1}$, respectively). Zone 5 exhibits the highest temporal variability in influx (SD of 38.2 particles $cm^{-2} yr^{-1}$) and also contains the lowest and highest influx values of the entire record (5 and 190 particles $cm^{-2} yr^{-1}$).

The type of charcoal (based on morphotype; Figure 6c) exhibits high intersample variability, particularly from 9200 to 1800 yr BP. During this time, the ratio of nonarboreal to total charcoal varies between 0.02 and 0.4, with three samples higher than 0.3. This indicates that fuel consisted of both nonarboreal (2–40% of the total charcoal) and arboreal (60–98% of the total charcoal) sources during this time but more strongly arboreal sources. From 1800 yr BP to present, the nonarboreal-to-total charcoal ratio is generally much lower than earlier in the record and varies between 0.01 and 0.17 (1–17% of the total charcoal is nonarboreal; 83–99% of the total charcoal is arboreal), indicating that fuel sources contained a higher proportion of arboreal material than earlier in the record.

Discussion

8200 yr BP transition

The shift in vegetation from deciduous woodland to grassland in the northern Great Plains at the beginning of the mid-Holocene is noted in many records across the region (Baker et al., 1992; Grimm et al., 2011; Schwalb and Dean, 2002; Van Zant, 1979), although the timing and magnitude of shifts vary. At Fox Lake, this transition occurs at approximately 8200 yr BP and corresponds with the final collapse of the Laurentide ice sheet (Shuman et al., 2002) as well as the documented 8200 yr BP event noted originally in the Greenland ice core records (Alley and Ágústsdóttir, 2005). In much of eastern North America, climate transitioned from

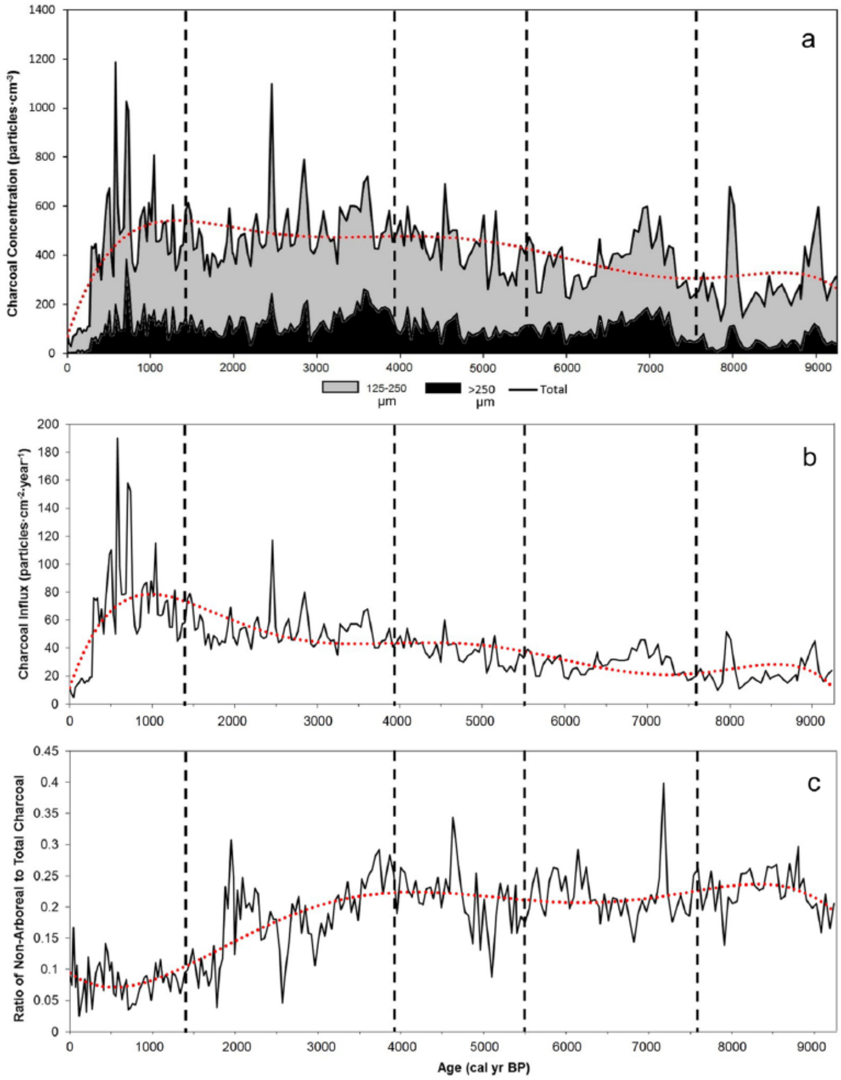

Figure 6. Charcoal data for Fox Lake, Minnesota, plotted against age (cal. yr BP). Panel (a) portrays the total charcoal concentration (particles cm^{-3}), the charcoal concentration of particles larger than 250 µm (particles cm^{-3}), and the charcoal concentration of particles 125–250 µm in size (particles cm^{-3}). Panel (b) portrays the total charcoal influx (particles $cm^{-2} yr^{-1}$). Panel (c) portrays the ratio of nonarboreal to total charcoal particles. All trendlines were defined by a sixth-order polynomial fit.

being partially controlled by ice sheets to being completely controlled by insolation at this time (Shuman et al., 2002). At Clear Lake (Baker et al., 1992), approximately 100 km east-southeast of Fox Lake, the transition occurred at approximately the same time as at Fox Lake. In the context of prevailing air masses, Baker et al. (1992) described this decline in deciduous woodland as corresponding with an increasing presence of dry, warm Pacific air in the region as identified by Bryson (1966). At Lake West Okoboji (Van Zant, 1979), approximately 50 km southwest of Fox Lake, the transition occurred slightly earlier (around 9000 yr BP), possibly due to Lake West Okoboji's more western position allowing it to be exposed to the dry, warm Pacific air earlier. However, the dates reported at Lake West Okoboji are uncorrected, as the record precedes current standard age-modeling techniques that include calibration of raw radiocarbon dates, so that could be a reason for the seemingly earlier transition. At Kettle Lake, approximately 850 km northwest of Fox Lake, the 8200 yr BP event is not strongly expressed, as a significant shift toward aridity had already occurred at 9250 yr BP (Grimm et al., 2011; Figure 3). Given the timing of the transition at these other sites in the region, Fox Lake is likely one of the most westernmost lakes of current calibrated records in North America exhibiting the 8200 yr BP event.

The large spike in *Ambrosia* pollen that occurred at approximately 8200 yr BP and followed the decline in *Ulmus* and *Quercus* pollen is indicative of an increase in disturbance events. This disturbance likely began as a drought or a series of drought events and was followed by a fire that consumed the dry biomass, as noted by the spike in total charcoal concentrations, regional charcoal concentrations (125–250 µm), and to a lesser degree local charcoal concentrations (>250 µm) that occurs shortly after 8000 yr BP. In the pollen, classic post-disturbance taxa such as *Iva* and *Xanthium* increase after the initial spike in *Ambrosia*. This supports previous assertions that the transition from the early to mid-Holocene was relatively abrupt compared with transition from mid- to late-Holocene (Nelson et al., 2004; Umbanhowar et al., 2006). At Fox Lake, *Ambrosia* percentages remain generally higher during the mid-Holocene than the early or late-Holocene, although they exhibit a great amount of intersample variability. These overall higher levels of *Ambrosia* are somewhat counter-intuitive given that *Ambrosia* is not very drought tolerant (Craine and McLauchlan, 2004; Grimm, 2001), and the mid-Holocene has been well established as being an arid time in the Great Plains. However, similar trends in *Ambrosia* at Kettle Lake during the mid-Holocene were attributed to intermittent humid years overlain on a background of drought conditions (Grimm et al., 2011). This could have been the case at Fox Lake as well.

Relationship between vegetation diversity and fire

Vegetation diversity. Diversity in the pollen data remained generally unchanged with fire activity or vegetation community type at Fox Lake throughout the record, as exhibited in both the pollen richness and pollen turnover indices (Figure 5a and b). Present-day grasslands in North America have been known to be floristically species rich due to their regular exposure to natural disturbances such as grazing and fire which reduce abundance of dominant species and promote growth of rare species (Hartnett et al., 1996). However, intense and frequent disturbances, particularly caused by droughts or frequent fire, have been found to reduce species diversity in grasslands (Collins et al., 1998; Tilman and Elhaddi, 1992). This could explain the large spread and intersample variability in richness of the pollen assemblages throughout the record (range of 13–30 pollen taxa per sample and a SD of 3.6), despite the lack of overall change in average richness. Drought and frequent fire could have prohibited growth of rare species on a frequent temporal basis, causing the vegetation community to be less diverse (the samples with lower total richness) than it could have been if subjected to less frequent or no drought or fire (the samples with higher total richness). This particularly makes sense in the context of recurring megadroughts throughout the Holocene being interspersed by humid periods (Cook et al., 2010; Laird et al., 1996a), allowing rare species to flourish during the time between large disturbances. Nevertheless, lack of change in average richness or turnover values throughout the record suggest that on a long-term basis, disturbances were not significantly altering the composition of the vegetation at Fox Lake. This remains true even during the mid-Holocene, when total pollen influx levels were lowest, and patches of bare ground were more likely to be present than at any other time during the record.

The low levels of taxonomic turnover throughout the record seem to indicate that the same types of plants were generally present during all temporal zones, albeit in varying amounts. *Quercus* is a good example of this because it was present in relatively large amounts early in the pollen record when it was a main component in the deciduous woodland at the site. During the mid-Holocene, it became much less abundant although still maintained a small presence in the assemblage. In the late-Holocene, *Quercus* was present in a more savanna-like environment as it began to gradually increase in abundance along with other tree taxa. *Quercus* pollen concentrations have also demonstrated high sensitivity to changes in available moisture ranging from savanna to forest conditions in pollen records in Wisconsin, to the east of Fox Lake (Mueller et al., 2014). Additionally, it is possible that turnover could have been occurring within a taxon and remained undetected in the pollen data, for example, a shift from C3 to C4 grasses. It is typically not possible to distinguish between C3 and C4 grasses based on pollen alone, but this is an inherent limitation of all pollen proxy data and is not exclusive to this study. Future effort should be directed toward understanding turnover rates in pollen data from grassland regions in order to provide more opportunity for direct comparison among sites.

Given the relatively large surface of the lake (385 ha; Figure 1), the pollen data from Fox Lake can be interpreted as an indicator of regional vegetation. Generally, larger basins represent regional vegetation, while smaller basins represent local vegetation (Sugita, 2007a, 2007b). It should be noted that other pollen records collected from grassland lakes in North America cover a wide range of surface areas, including some that are much larger in size than Fox Lake, such as nearby Lake West Okoboji (1500 ha; Van Zant, 1979) or Clear Lake (1500 ha; Baker et al., 1992, 2002), and some that are much smaller, such as Amber Lake (72 ha; Umbanhowar et al., 2006) or Kettle Lake (2.2 ha; Grimm et al., 2011). In essence, Fox Lake falls in the middle of this range, but lake size should be taken into consideration when interpreting the context with other work in this region.

Fire and fuel sources. Despite the clear indications from pollen that Fox Lake was in a prairie biome, dominated by herbaceous plants from at least 8000 to 2500 yr BP, the charcoal morphotypes demonstrate persistence of woody fuels throughout the Holocene. In landscapes with both grass and trees, fire plays an important role in determining vegetation structure (Staver et al., 2009). Fluctuations in the nonarboreal:total ratio of charcoal have been observed at oak-savanna sites in Wisconsin during times in the Holocene when no change in vegetation occurred (Mueller et al., 2014). In addition, woody plants in a frequently burned grassland may be overrepresented in charcoal morphotype production (Leys et al., in review).

The charcoal morphotype data at Fox Lake do indicate an increased presence of arboreal fuel sources in the most recent part of the record – 1800 yr BP to present (low nonarboreal:total ratio during that time; Figure 6c). This could be explained by the increasing presence of trees resulting from late-Holocene moisture increases, but this increased presence could take several forms, including shrub growth in wet prairies, trees on the perimeter of the lake, or even woody patches within the region. Indeed, large woody areas and fertile prairies were noted near Fox Lake in 1838 CE, in addition to heavily timbered riparian areas in the region (Bray and Bray, 1976). Given the relatively large size of Fox Lake, arboreal charcoal could have originated from these areas even if the sources were not within the immediate vicinity of the lake. Another possible source could be *Salix* sp. or *Cornus* sp.; woody taxa that were likely common in wet prairies during that time and are still present around the lake today. Also at 1800 yr BP, a higher degree of intersample variability begins to appear in the local charcoal concentrations and influx. This suggests a change in the fire regime, such as changes in intensity or area being burned. Further study of grassland fires and their signature in sedimentary charcoal would be helpful to determine whether herbaceous plants were truly less abundant on the landscape during this time relative to other times or whether their charcoal is simply underrepresented.

The charcoal concentrations at Fox Lake are generally higher during grassland times than during the woodland part of the record (Figure 3). This difference is more distinct in the local charcoal (>250 μm) than the regional charcoal (125–250 μm; Figure 6). The higher concentrations of charcoal exhibited during grassland times could be due to combustion dynamics, with low-temperature fires producing incomplete combustion of both woody and herbaceous fuel sources (Sikkink and Keane, 2012) and, therefore, a high quantity of charcoal pieces. Alternatively, high charcoal counts could reflect local area burned, which seems to be the case for grasslands in the southern Great Plains region (Leys et al., in review).

It is not completely clear whether fire responded to mid-Holocene aridity, but fluctuations in charcoal concentrations during the mid-Holocene could indicate that fuel quantity or quality varied quite a bit throughout that time, despite the lack of change in vegetation composition or diversity. In addition, charcoal concentration exhibits a moderate inverse relationship with both total pollen influx and nonarboreal influx (Table 2) seeming to indicate that fire activity was greater during times of less vegetation. If the lower levels of pollen influx actually do equal less biomass present on the landscape than in the earlier, forest part of the record, grassland fuel quality must have been very high (i.e. highly flammable) compared with earlier times. This matches well with known regional climate conditions being more arid during the mid-Holocene (Grimm et al., 2011; Figure 3). Alternatively, given the size of the lake and the likely regional vegetation signal represented by the pollen (Sugita, 2007a), it is possible that biomass quantity could have been limited in other areas of the pollen source area but not limited locally. Still another possible explanation is that the low pollen influx values could be a result of in-lake dilution from increased aquatic productivity, given that %C increased (albeit very slightly; Figure 3) during the mid-Holocene and %Si remained relatively high (around 20.5–21.5%).

From 8000 to 4000 yr BP, local charcoal concentrations are generally higher than during the early Holocene, possibly indicating that fires in the catchment were not fuel-limited overall (by fuel quality or possibly fuel quantity). However, local, regional, and total charcoal concentrations all increase from 7800 to 7000 yr BP but then decrease until approximately 6000 yr BP, so fuel availability could have diminished during that time. The gradual increase in local, regional, and total charcoal concentrations after 6000 yr BP seems to indicate that fuel availability gradually increased again and matches well with the pollen influx data. The local charcoal concentrations exhibit an obvious increase until 3600 yr BP which is not shown in the regional charcoal, supporting the idea that fire activity in the region probably varied significantly at the local level (Camill et al., 2003; Umbanhowar et al., 2006).

Variation in magnetic susceptibility

Magnetic susceptibility can be complicated to interpret in the context of climate, vegetation, or fire as it is not a direct proxy of any of these things. At Fox Lake, magnetic susceptibility increases in zone 1 as arboreal pollen begins to decrease and the vegetation transitions from a deciduous forest to a grassland. A similar trend was also exhibited at nearby Kimble Pond and Sharkey Lake as the vegetation shifted from oak savanna to grassland and led to an increase in magnetic minerals from either eolian input or soil erosion (Geiss et al., 2003).

The generally high, yet quite variable, magnetic susceptibility values continue into zone 2 at Fox Lake, although the source (whether from eolian input or soil erosion) of this increased input of magnetic minerals still remains unclear. At Kimble Pond and Sharkey Lake, the high and variable susceptibility values during the mid-Holocene are all attributed to eolian deposition (Geiss et al., 2003). Additionally, across the Great Plains, the mid-Holocene has been well demonstrated to have been the driest time during the Holocene with persistent, recurring megadroughts and/or low effective moisture at several sites, including in Nebraska (Schmieder et al., 2013), North Dakota (Grimm et al., 2011; Laird et al., 1996b), and Minnesota (Bartlein and Whitlock, 1993). Given these regional trends in aridity, it seems unlikely that the high levels of magnetic minerals in Fox Lake during this time would be attributed to alluvial transport, and much more likely that they would have resulted from eolian deposition. In addition, severe droughts can destabilize the landscape by hindering the growth of vegetation and enabling greater influx of sedimentary material into lakes (Lascu et al., 2012). However, Geiss et al. (2004) found that the magnetic signal of drought can be rather complicated, so it is difficult to say with certainty whether the high values in magnetic susceptibility at Fox Lake were due to eolian or alluvial transport during this time.

The most puzzling part of the magnetic susceptibility record at Fox Lake begins at approximately 5500 yr BP and continues throughout zone 3 and zone 4, where values drop very low (near $0\ SI \times 10^{-5}$) and remain low until approximately 1750 yr BP. These low values could be attributed to a number of factors, including a change in effective moisture, changes in eolian activity, or in-lake dilution from aquatic productivity. No dramatic changes are noted in the pollen or charcoal records at the time of the change in magnetic susceptibility around 5500 yr BP. However, as a whole, magnetic susceptibility is moderately inversely correlated with %C ($r=-0.53$; Table 2), and sediment deposition rates gradually increased during this time (Figure 2), suggesting a potential shift from clastic to more organic sources of deposition possibly resulting from increasing in-lake productivity. A very similar inversely correlative relationship ($r=-0.603$) was found between magnetic susceptibility and organic carbon at Pickerel Lake (Schwalb et al., 2010). They suggested that the periods of increased productivity occurred during calmer and wetter periods, while high magnetic susceptibility values occurred during periods of increased eolian activity. This could be what was occurring at Fox Lake as well.

Additionally, although fire has been found to increase magnetic susceptibility in soil (Gedye et al., 2000), fire does not appear to be related to the magnetic susceptibility values at Fox Lake. No significant correlation was found between these two proxies. Fire activity increased (Figure 6) at Fox Lake during zone 3 and seemingly decreased during zone 4, but the fires were insufficient in intensity to cause increases in magnetic susceptibility, which is typical of low-intensity grassland fires due to low amounts of biomass (Roman et al., 2013).

Conclusion

Aside from the abrupt shift in vegetation composition around 8200 yr BP, little change in vegetation composition occurred at Fox Lake throughout the mid- and late-Holocene. Pollen diversity remained relatively unchanged throughout the record, despite persistent fire activity and changes in total pollen influx. The persistence of woody charcoal during the mid-Holocene despite the indication in the pollen data that the landscape was a grassland supports the clear need for more charcoal records in this region to better understand the mechanisms involved in sedimentary charcoal deposition in grasslands. Additionally, an increase in magnetic susceptibility in the early part of the record occurs as vegetation shifts from woodland to grassland, while low values later in the mid-Holocene are more difficult to interpret and could be attributed to multiple mechanisms. Further multi-proxy analyses combining both magnetic and nonmagnetic proxies in this region are essential in order to better establish grassland vegetation, fire, and erosion dynamics in the context of Holocene climate.

Acknowledgements

We thank Amy Myrbo, Kristina Brady, and Joe Williams for coring assistance, and Scott McConaghy, Aaron Lingwall, and Troy Ocheltree for laboratory assistance. We also thank Christoph Geiss, Charles Umbanhowar, and an anonymous reviewer for helpful comments on this article.

Funding

This article was supported by the National Science Foundation CAREER grant (NSF BCS-0955225) to KM. LacCore (NSF IF-0949962) provided logistical support. A GK-12 fellowship (NSF DGE-0841414, PI Ferguson) supported JC during the 2014–2015 academic year.

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